Winter as a Factor in the Xerophily of Certain Evergreen Plants

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WINTER AS A FACTOR IN THE XEROPHILY OF CERTAIN EVERGREEN ERICADS[1]

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(WITH TWELVE FIGURES)

Of late years considerable attention has been drawn toward the apparently anomalous condition of several plants with obvious xerophytic modifications living in bogs with an apparently unlimited water supply. Many explanations of this apparent anomaly have been attempted. It was with a desire to obtain further knowledge upon the question that the author entered upon this piece of research work in the Botanical Department of the University of Michigan in the fall of 1910.

The work was carried on under the direction and supervision of Professor F. C. NEWCOMBE. To him I am greatly indebted both for the opportunity to work and for his stimulating criticism throughout the work. To Dr. H. A. GLEASON and to Dr. J. B. POLLOCK, both of the University of Michigan, I am also indebted for helpful conferences during the course of the work. To Mr. W. B. MCDOUGALL, of the University of Michigan, I am further indebted for the examination of material for the presence of mycorhiza. The nomenclature is that of the seventh edition of GRAY'S *Manual*.

[1] Contribution from the Botanical Laboratory of the University of Michigan, no. 136. The part of this work done during the summer of 1912 was carried on with the aid of a grant from the American Association for the Advancement of Science.

General discussion

In order to maintain existence, it is necessary for an organism to fulfil the fundamental requirements of life; it must be able to take in food; it must be able to digest its food; it must be able to oxidize or otherwise rearrange its substance to obtain energy; it must be able to eliminate its waste products; and it must be able to perpetuate its kind. Further, it must be able to perform all these functions in its particular, individual environment. As these individual plants cannot migrate, they must be able to accommodate themselves to the changing environmental conditions or die. That they flourish from year to year in healthy condition is unquestionable evidence that they are able to cope with their environment. Their ability to invade genetically lower associations of plants indicates that they are thriving rather than just merely existing in their habitat.

Although a living plant is always the expression of the integration of environmental and hereditary factors, the most important single factor in the environment is the physiological water supply. The modifications of plant structure which lead to the conservation of the water supply are termed *xerophytic adaptations* or *xerophytic reactions*. The presence of xerophytic adaptations does not necessarily predicate that the amount of water used by the plant is relatively small, but that the ratio of the amount used to that which the plant obtains tends to become less than unity. Some so-called xerophytic plants use as much or more than ordinary mesophytic plants, as GROOM (20) found was the case with *Larix decidua*. They are xerophytic, however, because they cannot absorb a large amount of water in proportion to that which they could otherwise transpire.

This is particularly true in the summer, when plants have their transpiring organs. The loss of leaves during the winter is quite rightly regarded as a xerophytic adaptation. The bog ericads which were investigated, however, retain their leaves during the winter. This opens at once the question, are these plants xerophytes because of their summer or their winter environment? As it may be safely assumed that the evergreen habit is hereditary in these ericads, the reaction to the environment necessitates the xerophily.

It would seem, at first glance, that plants which grow in bogs, where there is an obvious physical water supply, would not be restricted in its use, but the various xerophytic adaptations argue for the conservation of water in the plant. This fact led investigators to ask why the plants could not make full use of the water present. Many answers have been attempted, and it seems quite likely that the true answer is a combination of the different reasons rather than any one. The problem presents an obvious result obtained from a bewildering mass of causes, whose interactions are not yet known.

The ability of peat bog plants to absorb water is limited on account of poorly developed, shallow root systems (FRÜH and SCHRÖTER 18), low oxygen content of the water (DACHNOWSKI 9 and HESSELMANN 23), low aeration (TRANSEAU 49, DACHNOWSKI 10, and FREE 17), root excretions (LIVINGSTON, BRITTON, and REID 27, and SCHREINER and REED 45, 46), bog toxins (LIVINGSTON 29 and DACHNOWSKI 9, 10, 11), the necessity of mycorhizal fungi in some species, the low temperature of the soil water (KOSAROFF 25, FRÜH and SCHRÖTER 18, and especially TRANSEAU 49), and biological processes rather than chemical differences in the soil (DACHNOWSKI 12). Much stress cannot be laid upon the acidity of the soil, as has been done by SCHIMPER (44), because of the findings of later investigations. The acidity is very low and differs in different bog associations (TRANSEAU 49). That acidity is a necessary factor in the soil for the growth of trailing arbutus (*Epigaea repens*) and of the blueberry (*Vaccinium corymbosum*) was most admirably demonstrated by COVILLE (6, 7), who found that poor aeration was usually the real cause of poor growth and not acidity. Acidity, however, may be inimical to certain crops. SAMPSON and ALLEN (42) found that, as a rule, some of the common acids accelerate transpiration, and that weak solutions often produce as marked effects as strong ones.

The water absorbed is conducted up through the stems. A study of stem structure would show whether the ericads differ essentially from other bog shrubs. In either case the ability to conduct water must be adequate, as the plants thrive. From the stem the water passes into the leaves, where the largest

part of it is vaporized and passes out of the plant through the stomates.

Xerophytic responses may be classified into means retarding transpiration in the leaves or transpiring organs, absorption in the roots, checking transportation in the conducting tissue, or provision for an accumulation of water. In the peat bog ericads used during the course of this investigation, xerophytic response is very evident in the leaves, but is not accompanied by water storage tissue, which makes the xerophytic structure more necessary on account of the poorly developed root sytem. The evergreen habit, with its relatively large exposure of leaf surface, calls for greater activity of the root system throughout the winter, for transpiration still continues even when the thermometer is below zero. That means to reduce the loss of water are all the more necessary under winter conditions is obvious.

Seasonal history of peat bog plants

EVERGREEN ERICADS

During the winter the leaves of all of the evergreen ericads, *Chamaedaphne calyculata*, *Andromeda glaucophylla*, and *Vaccinium macrocarpon*, are upright, a position in which they receive a minimum of direct sunlight. The leaves are dark red or brown in color. With the coming of spring the old leaves curve outward or downward, resulting in an increase of the direct sunlight which they receive. At the same time the leaves become dark green in color. The season's growth of young leaves takes place soon after flowering. At first the young leaves are upright, but in a short time they bend outward. As soon as the young leaves are fully developed, the old leaves gradually drop off. In the case of *Vaccinium macrocarpon*, however, some of the leaves may be retained for two or three years. With the coming of the next winter, the leaves of these plants gradually bend up into an upright position and their color changes from bright green through dark green to shades of red and brown. The color changes begin at the margins of the leaves and work toward the midribs. In a mild winter the basal portion of midribs of *Chamaedaphne* may remain green the entire winter. *Vaccinium* and *Andromeda* are usually protected by a covering of

snow, but they exhibit these changes of position and color irrespective of that fact.

DECIDUOUS TREES AND SHRUBS

The principal trees are *Larix laricina* and *Acer rubrum*, and the commonest shrubs are *Aronia melanocarpa*, *Salix pedicellaris*, *S. discolor*, *S. sericea*, *Spiraea salicifolia*, *Betula pumila*, *Nemopanthes mucronata*, *Ilex verticillata*, *Gaylussacia baccata*, *Cornus paniculata*, *Cephalanthus occidentalis*, *Sambucus canadensis*, and *Rosa carolina*.

During the winter, bog trees and shrubs are leafless, which greatly reduces the transpiration. The snow that is present during the winter protects the root system and lower part of the stem from danger from excessively low temperature, but the upper parts of the trees and shrubs are not so protected. They must be able to resist water loss through their own modification. This is sufficient for the severest winters in southern Michigan. During the winter of 1911–1912, *Spiraea* was the only deciduous shrub to be killed down to the snow line.

With the opening of spring the buds swell and develop into branches bearing leaves which carry on the work of the season. A separation layer is formed upon the approach of winter at the base of the petiole, and by the time winter has set in the leaves have fallen.

HERBACEOUS PLANTS

The seasonal history of the herbaceous bog plants follows two general lines: the plant which has developed during the growing season may die down completely before winter, leaving seeds to reproduce it the following year, or it may die down to the ground and be vegetatively reproduced the following year from underground stems, bulbs, rootstocks, or buds. Any of these ways is an absolute xerophytic adaptation on account of winter conditions, but does not interfere with summer development.

Structure of certain peat bog plants

ROOT SYSTEM

Without exception, all of the forms dealt with had a very shallow root system, which was usually very poorly developed. It is in direct contrast to that of the xerophytes of the desert (CANNON 4).

Two general types of roots could be separated, according to the presence or absence of mycorhizal fungi. Most ericads have mycorhiza, but none were found upon the roots of *Andromeda* or *Chamaedaphne*. In working over the material furnished him by the author, McDOUGALL found that *Andromeda* occasionally gave evidences of mycorhizal appearance, although further investigation failed to reveal its presence. Mycorhiza was found on *Larix laricina*, *Acer rubrum*, and *Vaccinium macrocarpon*, but was not noticed on any of the following plants: *Carex filiformis*, *Sagittaria latifolia*, *Eupatorium perfoliatum*, *Dulichium arundinaceum*, *Asclepias incarnata*, and *Aspidium thelypteris*.

The absence of mycorhiza on *Chamaedaphne* and these other plants demonstrates that it is not a necessary adaptation to the bog environment. The presence of resin deposits (TRANSEAU **49**) is often a noteworthy feature of the roots of bog plants. Root hairs were not observed, although TRANSEAU (**49**) found that in culture solutions, which were well aerated, normal roots with root hairs were produced in *Larix*.

During the summer, the roots of the bog plants, at least apparently, have an abundant water supply, although as a matter of fact the *Sphagnum* which surrounds the roots may be physiologically dry, even when apparently wet, on account of its great ability to soak up and retain water (FRÜH and SCHRÖTER **18**, and DAVIS **14**). In general, however, there is standing water beyond the ability of the *Sphagnum* to absorb, and therefore the bog plants have a supply to draw on throughout a normal season. Seasons of drought, therefore, would be the critical ones, and that of 1911 was a case in hand. In so far as could be observed, it did not appear that the ericads were suffering from lack of water even on the hottest and driest days. The leathery nature of their leaves makes it nearly impossible to tell whether the plants are wilting or not, even when herbaceous vegetation was obviously wilted. In the natural distribution of these plants, droughts are not sufficiently extreme nor of sufficient duration to dry out the *Sphagnum*. The great ability of *Sphagnum* to soak up and retain water localizes the water within reach at the expense of the surrounding area. During the summer this often results in the elevation of the water table

under the bog several inches above that of the surrounding country.

Taking into consideration the rarity of real drought conditions of long duration, it is evident that the root system in the bog habitat is able more than merely to maintain these plants within their normal range throughout drought conditions. The xerophytic adaptations of the transpiring organs, of course, materially aid by lessening the demand upon root absorption.

During the winter the ground is normally frozen. On account of the low position of bogs, they are more subject to early and late freezes than the surrounding country. Although the ground may be frozen, the covering of snow prevents the access of very low temperatures to the roots. In spite of the fact that the ground is frozen, it is evident from the continual water loss of the above-ground parts that some water is being absorbed by the roots, quite likely the water vapor evaporated from the ice into the spaces which become opened around the roots soon after the freezing of the ground.

At any of the temperatures at which roots were dug up (down to -10° C.) it did not appear that any part of the plant was frozen. All parts were pliable to handling. The exposure of severed parts of *Chamaedaphne* for one-half an hour to -25° C. resulted in freezing and loss of pliability. It was repeatedly noticed that the leaves which had been exposed to the severest weather of the winter, including a temperature of -29° C., were dry, and cracked when bent. Later it became evident that these leaves had been killed. Beyond this simple test, whose limits of accuracy are not known, there were no suitable means of determining in the field whether the plant tissue was frozen.

CONDUCTING SYSTEM

The conducting system in bog ericads consists of a very narrow ring of young xylem just outside the old wood (fig. 1). There is a very striking similarity in the appearance of the cross-section of the three ericads studied. The type of stem represented in bog ericads is strikingly different from that of other bog shrubs in the relatively smaller amount of conducting tissue and in the smaller

lumina of its cells. In this respect bog herbs are all different from the bog ericads also. Among the bog shrubs the ericad type stands out distinctly from all the other shrubs, there being far less difference between the structure of any two ericads than between an ericad and any other bog plant.

Just how the water is conducted from the roots to the transpiring organs is not a closed question. For a discussion of it the reader is referred to the literature, particularly COPELAND (5), DIXON (16), OVERTON (37), RENNER (41), SCHERMBEEK (43), and BABCOCK (1). The results of this investigation show that the fundamental control of rate of conduction is exercised by transpiration. An increase of transpiration always means an increase of conduction, and a decrease in transpiration means a decrease in conduction, though not always in the same proportion. Absorption and conduction are more closely related to each other than to transpiration, and they are more closely related to the turgidity of the cells than is transpiration. By reducing the turgidity of the cells transpiration exercises a control over the other two.

FIG. 1.—Photomicrograph of the stem of *Chamaedaphne calyculata:* the dark outer ring is cortex, just within it is the medium colored young xylem, then the light colored wood, and in the center the pith.

UTILIZATION SYSTEM

Although the external appearance of the leaves of various peat bog plants is very different, the general internal structure is more nearly similar, and that of the various ericads is still more alike. Several well marked xerophytic adaptations are present, notably the strongly cuticularized epidermis, absence of stomates on the upper surface, a well developed palisade layer one to three cells thick, frequently sunken stomates, and coatings of wax, bloom, hairs, or scales. Mechanical tissue is present and accounts for the suppression of the ordinary symptoms of wilting. Usually the

leaves are at least slightly revolute, those of *Andromeda* and *Salix candida* strongly so. The leaves are usually dark green in color, but often reddish at the beginning and close of the vegetative season. The abundant presence of cutin in the evergreen ericads as an efficient xerophytic adaptation against loss of water at all times, but especially in winter, has been brought out by WIEGAND (51).

A considerable amount of water is transpired by many bog plants, and the loss may be as great as or greater than that from mesophytic plants of the same vicinity. This suggests that it is the maximum rate to which the plant may be subjected rather than the amount of water lost that is the important consideration. If the amount of food material is correlated with the amount of water lost, there would have to be considerably more water absorbed in the bog habitat, as it is notably deficient in available mineral food material (TRANSEAU 49). Plants that normally grow in non-bog conditions, as white pine and black spruce, when growing under bog conditions are much dwarfed and stunted, and their leaves exhibit very pronounced xerophytic modifications, so much so that these plants growing in bogs have received specific designation.

Some plants, as *Populus tremuloides* and *Poa pratensis*, that may grow in either bog or mesophytic soil, do better in the latter situation and always exhibit a pronounced xerophily in the bog soil. Some plants demand bog conditions and even then have xerophytic modifications, as COVILLE (6) demonstrated in the case of the blueberry.

During the growing season, all of the bog plants have their transpiring organs, but the great majority do not retain them during the winter. In every case where leaves are retained, their winter position is different from their summer one. The winter position is usually upright, but in the evergreen conifers the leaves are more closely appressed to the twig. The young leaf as it comes out in the spring is also upright and remains so at least as long as it is tender. The fact that the dark upper surface is innermost when the leaves are upright serves to protect it by reducing the amount of radiant energy absorbed, which would raise the temperature of the mesophyll cells and lead to greater loss of water. The under surface is already well protected. The upright, upper surface to upper

surface position of the leaves during winter is really a xerophytic modification, reducing the amount of radiant energy absorbed at a time when it would be needlessly dissipated in increase of water loss, which the absence of phytosynthesis and the closure of the stomates does not occasion. Leaves which develop upon *Chamaedaphne* in the *Larix* association are much less xerophytically modified. They are much more subject to winter killing.

The loss of water by the leaves exercises a twofold function. The excess of radiant energy absorbed and not used in photosynthesis could easily raise the temperature of the leaf to the death point during hot waves, were it not dissipated in vaporizing water. DARWIN (13), through the use of a resistance thermometer, demonstrated that, with the check to transpiration that comes with induced closure of the stomates, the temperature of the leaf rises. Normally this higher temperature would not occur, for the excess of radiant energy being used to vaporize water causes a lowering of temperature. The loss of water in the leaves maintains a stream of water from the roots up. This is necessary for the removal of the products of respiration (BABCOCK 1) and for the lifting of the absorbed mineral material to the leaves. Water is also necessary in photosynthesis.

As LIVINGSTON (30) puts it: "The total amount of transpirational water lost from a plant, for any given period, may be considered as a summation of the effects of the evaporating power of the air and of the radiant energy absorbed throughout the period, modified by certain secondary effects of these conditions and certain responses to other conditions." The ratio of the water income to that of the removal must not fall below unity for any considerable time in plants which are not water-storing. Quoting again from LIVINGSTON (31): "The really crucial question with regard to any soil . . . . is . . . . *at what rate, and for how long a time, can it deliver water to a unit area of a water-absorbing surface?*" That water is supplied in sufficient quantities during the most extreme conditions of summer that obtain in nature in this region is evident from this investigation. The opposite statement is true for winter, namely, that in very severe winters the removal of water from the exposed parts of certain plants is so in excess of the supply that too

thorough drying and therefore death result. This same process has already been shown by KIHLMAN (24) to be the cause of the arctic tree line.

That the water supply for ericads in Michigan peat bogs is actually ample to their needs is clearly demonstrated by experimentation upon potted plants, for even under the very extreme evaporating power of the air on July 5, 1912, the maximum rate of transpiration was contemporaneous with the maximum evaporating power of the air. Conditions of atmospheric evaporating power in Michigan are never as high as those of Arizona, where LLOYD (32) found that the fall in the rate of transpiration in ocotillo (*Fouquieria splendens*) occurred before that of the maximum evaporating power of the air. Whether these results may be the true expression of the behavior of rooted plants may be open to question, as LLOYD used cuttings to experiment with. It was found in the present investigation that on days of extreme evaporating power in Michigan a decline in the transpiration rate in advance of the time of maximum evaporating power of the air did actually occur in cuttings, but was not exhibited in potted plants of the same species. Such a check in transpiration is occasioned by what LIVINGSTON and BROWN (28) have termed "incipient drying," in the course of which the evaporating menisci have retreated into the pores of the cells, thereby not only decreasing the amount of the exposed surfaces, but also greatly increasing the surface tension of these evaporating surfaces, which decreases the vapor tension and consequently the rate of vaporization (RENNER 39, 40, and PATTEN 38). The increase in the concentration of cell sap which accompanies this check in water removal further retards vaporization. A very serviceable pictorial presentation of the matter is given by MACDOUGAL (34).

The recent work of some investigators seems to withdraw the foundations from the theory of the efficient function of the stomates as the regulators of transpiration (LLOYD 32, 33, and others). That closed stomates are efficient means of lowering transpiration has been demonstrated by many authors (BURGERSTEIN 3, and DELF 15). The closure of the stomates of evergreen plants during winter, which has been demonstrated by several investigators,

especially STAHL (47), is an important factor in reducing transpiration at that season, when the water intake is at best very low. The work of LLOYD (32) on *Fouquieria* led him to conclude that the capacity of the diffusion of the stomates was well in excess of what would be required for the greatest observed transpiration rate. F. DARWIN (DELF 15), in a preliminary account before the British Association, concluded that if the stomates can be observed by a sufficiently delicate method, the stomal movements will be found to correspond closely with changes in the rate of transpiration caused by alteration in external conditions.

In the present investigation, in which the method of relative time of penetration of an oil was used to indicate the condition of the stomates, there was no evidence that the stomates exercised a "closely regulatory" function. The stomates opened in the morning, in general in the diffused light of dawn, but the rate of transpiration showed no sudden rise, but rather kept proportional to that of the evaporating power of the air. In the afternoon the stomates did not begin to close until after the beginning of the decline in transpiration. This was true both in potted plants and in cuttings properly cared for on days that were not extreme. In many cuttings the closure of the stomates seemed to be due to the shock of cutting rather than to any excessive water loss. Almost all of the wilted plants had their stomates closed, but in dried leaves the stomates were open.

The experimentation on plants in the field led to the conclusion that the stomates were open during the hours of sunshine, and that, although the opening of the stomates preceded the rise in transpiration in the morning, the decline in transpiration set in in the afternoon before the beginning of closing of the stomates. The rate of transpiration sank more quickly to a lower level than the time it took the stomates to close could possibly account for.

Experimentation

MATERIALS AND METHODS[2]

Throughout the study of this problem an experimental method was used which yielded numerical data. The experiments were carried on upon bog plants, principally *Chamaedaphne calyculata*

[2] Cf. BURGERSTEIN 3.

(L.) Moench, obtained from First Sister Lake, a little west of Ann Arbor, Michigan, and at Mud Lake in the northern part of Washtenaw County, Michigan.

Toward the close of autumn in 1910 and 1911, plants of the evergreen ericads were potted and kept outdoors under prevailing conditions. During the middle of winter their transpiration was determined by successive weighings on a beam balance sensitive to 0.002 gram. The pot was inclosed by an aluminum shell (devised by GANONG) closed at the top with rubber dam and sealed with wax, whereby the water loss was limited to the plants, as controls repeatedly demonstrated. Readings of weight to 0.01 gram, temperature by mercury thermometer and thermograph, relative humidity by wet and dry bulb thermometers, and general conditions of the weather were recorded.

A number of pottings of ericads and other plants were made at First Sister Lake, June 1, 1912, the plants allowed to develop under bog conditions, and experimented upon the first week of July 1912.

By far the greater part of the work, however, was conducted with cuttings. These were made from the plants at First Sister Lake, immediately cut under water in jars and brought into the laboratory where they were again cut under water. The cuttings were then set up in two-holed rubber corks in bottles of distilled water and sealed with vaseline. A thermometer inserted in the other hole of the cork gave the temperature of the water. Work with controls proved that the apparatus was water-vapor tight. Usually about one-half an hour was allowed for adjustment before measurements were commenced. Weighings were made at intervals of one, two, or more hours, according to the purpose of the experiment. Such experiments were seldom carried over 24 hours, except for special reasons. The day of 24 hours of 100 "minutes" each was used in recording experiments, because of its obvious convenience.

Some plants which were transplanted into the greenhouse in *Sphagnum* did so poorly that no experiments were made upon them. Shoots that developed on cut twigs kept in water in the laboratory or greenhouse seldom lived more than a couple of weeks, and as their internal structure was not normal, no experiments were performed upon them.

It was found that different *Chamaedaphne* plants from the *Chamaedaphne* association (fig. 2) transpired at virtually the same rate during the same experiment. Consequently, that plant was taken as the basis for all comparisons and was included in practically every set of experiments.

With the close of the experiment the leaves were detached, placed side by side on white paper, covered with a thin piece of glass, and their outlines traced with a polar planimeter, by which means the leaf area was obtained. After a little practice with this instrument it was found that successive determinations of the same set of leaves did not vary by as much as 0.3 per cent. Accordingly the average of two determinations was used throughout the work. When stomates were also present on the upper surfaces (the rare exception in the plants used), the area thus obtained was doubled.

With the data so recorded, the results of each experiment were calculated with the aid of a slide rule to a standard basis, the rate of transpiration in grams per hour per 100 sq. cm. of leaf surface. These results were plotted on cross-section paper and the comparison made. As more than one determination for each plant was made, the resulting curves should approach a general similarity. Under the same conditions the similarity of the graphs was striking. Through dissimilarity of the resulting graphs, it was possible both to demonstrate the effect of change of experimental conditions and to weed out aberrant plants. As the greater part of the work was concerned with relative values, the continued reappearance of the same result in the graphs was taken to uphold the contention and no contention not thus uniformly upheld is presented in this paper.

During a part of the year 1912 the volume of the leaves was also determined by ascertaining the amount of alcohol they displaced. Alcohol was used in place of water on account of the large amount of air coating the leaves submerged in the latter. The results were calculated on the basis of water loss per hour per 1 cc. of volume. This was done in order to incorporate the results obtained from plants, the difficulty of determining the leaf surface of which would otherwise have rendered it virtually impossible. The correlation

of volume and leaf surface was irregular. With leaves of about the same size and thickness, the amount of water loss varied proportionally. In plants of *Chamaedaphne* from different plant associations, where both size and thickness of the leaves varied (fig. 2), it did not usually appear that volume was any constant function of the leaf area.

While it is recognized that the measured leaf area is not the area of the water-losing mesophyll cells, it is believed that it furnishes

FIG. 2.—Twigs of *Chamaedaphne calyculata*, showing the character of the leaves developed in the *Larix* association (bottles 1 and 2) and in the *Chamaedaphne* association (bottle 3), at First Sister Lake; April 29, 1911.

a satisfactory basis of comparison attained without the excessive difficulty that would attend the determination of the actual area of the surface abutting upon the intercellular spaces. The leaf surface, moreover, is the area through which the diffusion into the outer air takes place.

To obtain a knowledge of the evaporating power of the air an open dish of water was run with several of the experiments.

At the close of many of the experiments a section of the smallest part of the stem below any transpiring organs was cut out,

preserved in glycerin-alcohol, later sectioned, and stained with iodin green to show the area of the conducting system.

By means of the lithium nitrate method, which consists of cutting off the lower ends of leafy stems under a 0.5 per cent aqueous solution of $Li(NO_3)_2$, allowing the stems to take up the solution, removing after certain intervals, and cutting immediately into 1 cm. lengths, testing these pieces in the spectroscope for the presence of lithium, a knowledge of the rate of conduction under different conditions was obtained. This method only approximates the rate of conduction in rooted plants, which could not be used because of inability to know when the lithium nitrate would be absorbed by the roots.

The difficulty of examining the stomates of *Chamaedaphne* by the ordinary method of stripping and the consequent uncertainty of its results with this species led to the abandonment of work on stomates until the publication of a new method (MOLISCH 35) opened the way for experimentation upon this pertinent question. The "infiltration method," as it is called, depends upon the fact that when a leaf is wetted with a penetrating liquid, such as absolute alcohol, xylol, or turpentine, and held up to the light, it becomes translucent as soon as the liquid has penetrated the leaf. The relative time that it takes the leaf to become translucent after the application of xylol indicates whether the stomates are open or closed, because the more the stomates are open, the easier and quicker will the liquid penetrate the tissue and the sooner will it become translucent. A "normal" time must be determined for each species upon which to base deviations. Xylol was used throughout the present work, and the results were checked up with absolute alcohol and turpentine. As the method is so very simple, it can be employed in the field and several determinations made each time. The results were remarkably uniform.

EXPERIMENTATION DURING THE WINTER

Transpiration

During winter the transpiration of the plants of the region is reduced to a serviceable minimum which, however, is not zero (cf. KUSANO 26). For herbaceous plants the minimum is lower

than for shrubs and trees. No experimentation was performed upon herbaceous plants during the winter, for it is known how exceedingly small is the amount of water loss from seeds, and as the vegetative means of reproduction employed by other herbs are

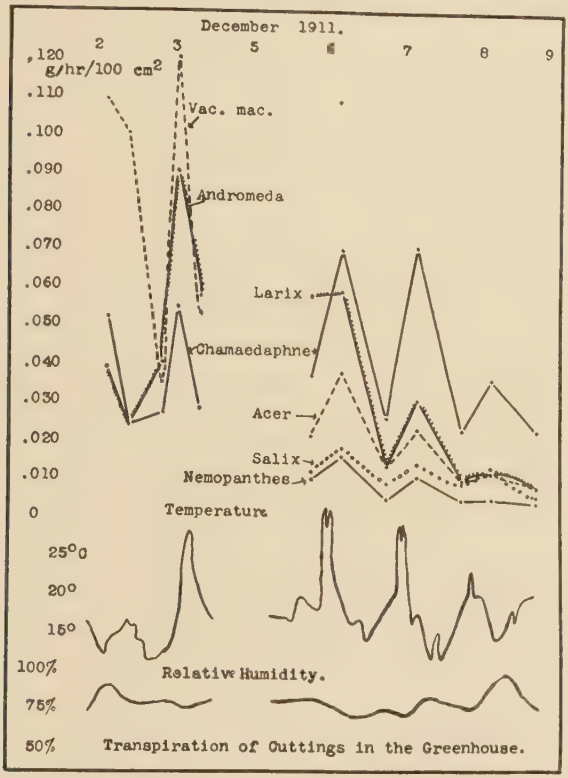

FIG. 3.—Transpiration of cuttings of *Acer rubrum*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Larix laricina*, *Nemopanthes mucronata*, *Salix pedicellaris*, and *Vaccinium macrocarpon* in the greenhouse.

underground and thoroughly protected from exposure, no comparison could be made with the ericads which retain their plant body subject to constant exposure throughout the winter.

The purpose of the winter experimentation, therefore, was to obtain a knowledge of the transpiration of several of the shrubs and trees, and compare that of the leaf-retaining ericads with that of the deciduous shrubs, under winter conditions outdoors and under

laboratory conditions which simulated the severest conditions which could obtain in nature during the winter.

Experimentation was carried on both with potted plants and with cuttings indoors and outdoors. A few of the graphs obtained from the data from these experiments are given in figs. 3–6. Although they have been selected from the general array of data to avoid needless repetition they represent the general conclusions, not merely special cases.

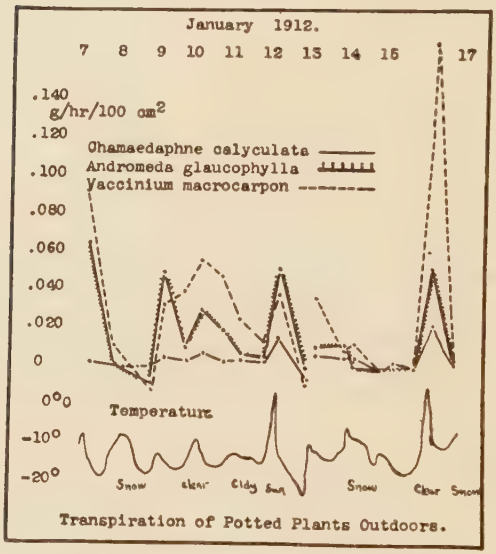

FIG. 4.—Transpiration of potted plants of *Andromeda glaucophylla*, *Chamaedaphne calyculata*, and *Vaccinium macrocarpon* outdoors in winter.

Consideration of these data clearly indicates that the transpiration of these bog plants is very low in winter. Furthermore, with scarcely an exception, the rate of water loss is much greater (2–15 times) in the evergreen ericads than in the leafless shrubs and trees. When the very much more exposed position of the deciduous trees and most of the deciduous shrubs is taken into account, the difference in the rate of transpiration in nature is accentuated. The mere position of the ericads near the ground serves to reduce water loss. This same relation holds among the ericads themselves, namely, that the greater the rate of transpiration under given conditions, the more protected is the position in which that species grows. For example, *Chamaedaphne* transpires at a lower rate than *Andromeda* and *Vaccinium;* and *Chamaedaphne*, because of its higher growth, is more exposed. YAPP (52) has shown that the nearer the ground in a closed association the lower the evaporating power of the air.

These data support the well known facts that transpiration

varies directly with the temperature, inversely with the relative humidity, and is greater in daylight than in darkness. The last may be almost entirely included in the two former, as the absorption of radiant energy during the day would increase the temperature of the leaf were it not used up in augmenting transpiration. For example, on February 27–29, with a temperature constant to within 2° and the relative humidity constant to within 5 per cent, in plants of *Chamaedaphne* which were run in the laboratory with light about 0.1 per cent of sunlight, not at any time being exposed to direct sunlight, the rate of transpiration was very noticeably higher (0.071 gm. and 0.083 gm.) during the diffuse daylight than in the periods of darkness before and after. During the night following, with the temperature constant but the humidity dropping slightly, the transpiration of these same duplicates decreased to 0.046 gm. and 0.060 gm. respectively.

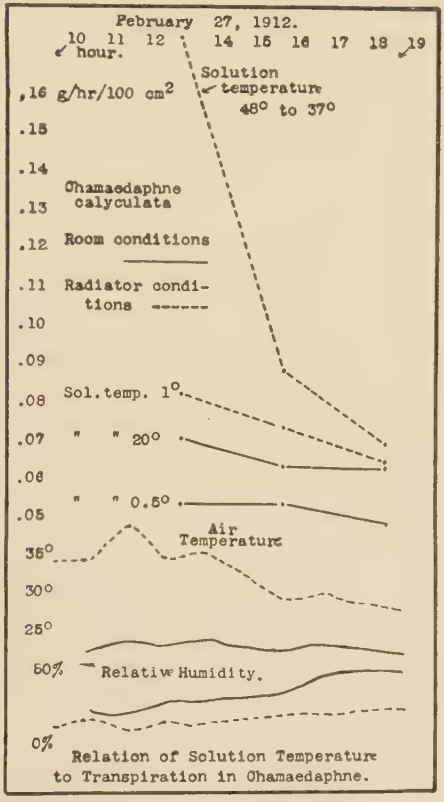

FIG. 5.—The relation of solution temperature to transpiration in *Chamaedaphne calyculata.*

Only rarely does the rate of transpiration exceed 0.01 gm./hr./100 sq. cm. in any of the plants experimented with under winter conditions. With the exception of *Vaccinium macrocarpon,* the rate was more often less than 0.005 gm. than above it. In the deciduous shrubs it was usually below 0.001 gm., and not infrequently was hardly within the power of measurement with

the means employed. The advantage of the deciduous habit in reducing transpiration in the winter is apparent.

Per unit area of leafless twig surface, bog shrubs lose less water than do the bog trees under the conditions of these experiments. Furthermore, bog shrubs are more subject to winter killing in a severe winter in this latitude unless protected by snow. This would seem to indicate that the xerophytism of the bog trees was in general more efficient than that of the bog shrubs under extreme winter conditions, or that their means of water renewal was more efficient.

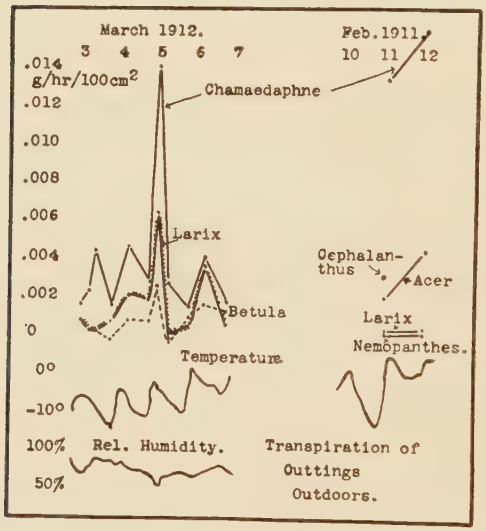

FIG. 6.—Transpiration of cuttings of *Acer rubrum*, *Betula pumila*, *Cephalanthus occidentalis*, *Chamaedaphne calyculata*, *Larix laricina*, and *Nemopanthes mucronata* outdoors in winter.

During stormy weather it is difficult to allow a real exposure to the weather and then be able to measure transpiration by weighing, but repeatedly, even when preparations were shielded from the rain or snow, measurement showed an increase in weight beyond that of a control. This was noticed particularly in *Chamaedaphne* and *Andromeda*, whose leaves were covered beneath with scales and hairs, respectively. This absorption helps replenish the saturation deficit of the leaves, and so in a measure alleviates the demands upon the root system at a time of year when absorption is at best difficult. It is not certain, however, whether this water absorbed from the air ever actually penetrates to the mesophyll.

Influence of solution temperature upon transpiration

To determine the influence of the temperature of the solution from which the cutting was taking water upon the rate of tran-

spiration, a number of experiments were made in the laboratory, the results of which are summarized in table I.

TABLE I

SUMMARIZING THE EFFECT OF LOWERING THE TEMPERATURE OF THE SOLUTION UNDER THE SAME EVAPORATING POWER OF THE AIR. THE TRANSPIRATION IS EXPRESSED IN GRAMS PER HOUR PER 100 SQ. CM., AND THE NUMBER OF MEASUREMENTS UPON WHICH THE AVERAGE IS BASED IS GIVEN IN PARENTHESES

Under room conditions (temp. 18–25° C.; rel. hum. 30–40 per cent)

	Solution at room temperature	Solution at freezing temperature
Chamaedaphne (Chamaedaphne association).....	0.062 (13)	0.054 (13)
Chamaedaphne (Carex association).....	0.080 (2)	0.068 (4)
Chamaedaphne (Larix association).....	0.042 (2)	0.042 (3)
Larix laricina (Larix association).....	0.022 (4)	0.028 (4)

Under radiator conditions (temp. 38–50° C.; rel. hum. 4–20 per cent)

	Solution at radiator temperature	Solution at freezing temperature
Chamaedaphne (Chamaedaphne association).....	0.141 (12)	0.067 (11)

In the course of these experiments cuttings were made during the cold snowy weather of February and March 1912, and subjected to different conditions in the laboratory. The laboratory conditions of temperature and relative humidity are more extreme than these plants are ever naturally subjected to in winter.

To determine the influence of a cold source of water supply, twigs were set up in water in bottles, set in a snow mixture, which kept the temperature of the solution at or near freezing. Other twigs set up in the room gave data for comparison. The general results show a lower rate of transpiration from the colder solution. The effect, however, is not so pronounced as might be expected. The control was much less perfect in leafless twigs than in leafy ones. Leafless twigs have occasionally shown a higher rate of transpiration from the colder solution. This is probably due to the stimulation which is the first effect of application of cold (BOSE 2). Such a higher rate, however, is only temporary, although it has continued for 10 hours in some of the leafless twigs experimented upon. Warming the solution was uniformly accompanied by a rise in the rate of transpiration. A lowering of the rate of

transpiration from a colder solution would be caused by the extra amount of energy required to warm the colder water up more degrees of temperature. In nature these bog plants are subjected to these extremes of temperature maintained in the laboratory, and this range is well within their physiological ability.

These experiments were repeated under the very severe conditions obtaining over a steam radiator. As the temperature of the solution became hot, transpiration proceeded at a very rapid rate, until the tissue was killed at a temperature of 42–46° C., after which the transpiration fell to a low amount without a corresponding drop in the evaporating power of the air. The graph obtained by plotting the data may be called the death curve. It is similar to those obtained by BOSE (2) in experimental work on death in plant tissues. After the marked drop, the rate of transpiration increases and then fluctuates with the evaporating power of the air, but does not exhibit the decided increase which the access of sunlight causes in living twigs.

Other twigs maintained in cold water under radiator conditions exhibited a higher rate of transpiration than those in the room. The average rate of transpiration under these conditions was very little in excess of that of twigs in the room with solution at room temperature. This clearly shows the retarding influence of cold soil water. It also shows the ability which these plants possess of withstanding a much severer aerial condition of high temperature and low relative humidity than they are ever subjected to in nature.

Rate of conduction of a 0.5 per cent aqueous solution of lithium nitrate

Table II summarizes the winter experimentation upon the rate of conduction in peat bog plants.

The results obtained from these experiments were subject to considerable variation, but in general the rate of conduction was greater from warmer solutions. Plants from habitats where the soil temperature is naturally lower seem to have a greater ability to conduct water from a colder solution. Transpiration takes place faster from a warmer solution. An increase of rate of conduction from a warmer solution is just what is to be expected to supply the greater demand for water which increased transpiration entails.

TABLE II

Under room conditions (temp. 18–24° C.; rel. hum. 27–45 per cent)

	Solution at warmer temperature (20°)	Solution at colder temperature (0°)
	cm./hr.	cm./hr.
Chamaedaphne (Chamaedaphne association)	3.1 (29)	2.5 (33)
Chamaedaphne (Carex association)	3.2 (13)	3.1 (12)
Chamaedaphne (Larix association)	3.5 (14)	4.3 (12)
Acer rubrum	0.8 (3)	0.6 (4)
Spiraea salicifolia	2.1 (2)	1.3 (2)
Betula pumila	2.4 (3)	2.0 (3)
Larix laricina	3.0 (17)	2.7 (19)

Under conditions found over steam radiator

	Solution at warmer temperature (40°)	Solution at colder temperature (0°)
Chamaedaphne calyculata	3.0 (9)	2.8 (9)
Larix laricina	5.1 (4)	....

Experiments that were run outdoors showed a rate of conduction less than 1 cm./hr. Conduction continued to take place even after the solution was frozen.

Relationship between rates of conduction and transpiration in evergreen ericads

Tables III and IV summarize the experimental results.

TABLE III

EXPERIMENTS OF APRIL 4–6, 1912

Rate of conduction in centimeters per hour

	Chamaedaphne calyculata	Andromeda glaucophylla	Vaccinium macrocarpon
April 4	5.90 (7)	7.5 (13)	.....
April 5	4.90 (9)	.....	8.3 (12)
April 6	.....	11.1 (12)	16.3 (11)
Average	5.34	8.43	12.11
Ratio	1.00	1.58	2.27

Rate of transpiration in grams per hour per 100 sq. cm. of leaf surface

	Chamaedaphne calyculata	Andromeda glaucophylla	Vaccinium macrocarpon
April 4	0.140 (2)	0.230 (2)	.....
April 5	0.101 (2)	.....	0.301 (2)
April 6	.....	0.290 (2)	0.527 (2)
Average	0.121	0.260	0.414
Ratio	1.00	2.15	3.42

TABLE IV

CHAMAEDAPHNE CALYCULATA

	February 27	March 1	March 3	March 5
Laboratory (room temp.)...	$\frac{0.067}{2.4}=0.028$	$\frac{0.051}{1.8}=0.028$	$\frac{0.043}{2.8}=0.015$	.....
Laboratory (sol. freezing) ..	$\frac{0.052}{1.9}=0.027$	$\frac{0.052}{2.3}=0.023$	.....	$\frac{0.060}{2.5}=0.024$
Radiator (rad. temp.).....	$\frac{0.111}{2.9}=0.038$	$\frac{0.199}{2.0}=0.099$	.....	.....
Radiator (sol. freezing).....	$\frac{0.073}{2.5}=0.029$	$\frac{0.61}{2.6}=0.023$	.....	.....
Outdoors (sol. frozen).....	$\frac{0.010}{0.5}=0.020$	$\frac{0.007}{0.8}=0.009$	$\frac{0.003}{0.7}=0.004$	.....

To obtain the factor in table IV, the average of the values of all specimens under the same conditions during a day was used as a unit. The rate of transpiration was divided by the rate of conduction. The resulting factor expresses the number of grams of transpiration per unit area, which is equivalent to 1 cm. of conduction. With the solution at a lower temperature in one of two simultaneous sets, but the evaporating power of the air the same, it takes smaller amount of transpiration to account for 1 cm. of conduction.

Utilizing the high temperature of the steam radiator in the laboratory, it was found that a much greater (2–4 times) amount of water loss occurred in proportion to the amount of conduction in plants kept in solutions at the radiator temperature than near freezing. The temperature of the radiator exceeded the death point of the plants and was far above any temperature that their roots are ever subjected to in nature.

Plants maintained in solutions near the freezing point in the extreme evaporating condition of the air above the radiator, a condition which is more severe, with respect both to summer heat and to summer soil water temperatures, than any ever experienced by *Chamaedaphne* in its natural habitat, exhibited a higher transpiration and a higher rate of conduction than plants kept in the room at both room and freezing temperatures. This was in spite of the cold solution. A comparison of the transpiration-conduction factor of plants in freezing solutions in the room and over the radiator shows scarcely any difference.

With cuttings experimented upon outdoors it took even less transpiration for a given amount of conduction.

The logical conclusion substantiated by these data is that the ability of plants of *Chamaedaphne* to conduct water is at all times, when above −15° C. (the lowest temperature at which experiments were performed), greater than the necessity, and that xerophytic modification in any part of the plant is not a result of the lack of ability to conduct water.

The occurrence of temperatures of −15° is frequent in the natural range of these plants and no injuries are apparent. At a temperature lower than −25°, such as occurred during February 1912, the drying up of the exposed leaves, twigs, and flower buds of *Chamaedaphne* is first hand evidence that at such a low temperature the conduction in the upper part of the plant is not sufficient to supply the transpiration demands.

Relation of winter to the xerophily of peat bog ericads

Among peat bog plants, ericads, with but few exceptions, retain their leaves during the winter, when most other plants are leafless. This is usually considered a matter of heredity. The presence of leaves very materially increases the evaporating surface of the plant and thereby enhances the demand for water from the habitat.

That the different ericads experimented with differed among themselves in their transpiring ability with their degree of protection from excessive evaporation during the winter, and that *Chamaedaphne*, the least protected, transpires considerably more than the leafless shrubs and trees, indicates both the effectiveness of the deciduous habit as a xerophytic adaptation and the necessity of there being other xerophytic modifications in the case of the ericads. Added to this, the difficulty of absorbing water is apparent, due, if for no other reason, to the colder temperature of the bog soil in winter, and the necessity of xerophytic modification. The presence of so many of the usual xerophytic modifications in these peat bog ericads is noteworthy. The thick cuticle, dense palisade layer, more or less sunken stomates, hairs, scales, bloom, and waxy coverings, resin, and the upright position of the leaves are all indications

of this xerophily, this necessity of keeping the transpiration within the limits of absorption and conduction.

From the experimental work it was evident that, supplementing any water vapor absorbed by the leaves, the rates of absorption and conduction in the evergreen ericads are more than ample to furnish sufficient water for transpiration during warm spells in winter and for continued periods of cold temperature down to at least $-15°$. When, however, continued temperatures lower than $-20°$ prevail in this region, the rate of conduction is not sufficient to prevent drying and death of the exposed parts of the plant. On this point the winter of 1911–1912 gave remarkable evidence. Consequently, a high degree of xeromorphism is demanded to compensate for a lack of a decrease of leaf surface during the winter.

EXPERIMENTATION DURING THE SUMMER

Transpiration

The water loss of plants is greatest in amount during the summer or growing season. The greater evaporating power of the air, the greater exposure of surface of most plants, the greater availability of water, and the use of water in photosynthesis all express the direct opposite of the conditions in winter and show the greater need for water in the summer. The results of a few typical experiments have been plotted in figs. 7–9.

During the first week of July 1912, the transpiration of three series of potted plants was determined at frequent intervals (fig. 10). As this week was one of extremely hot, dry weather, it will serve to indicate the limits of transpiration to which these plants may be subjected in summer. At the beginning of each series of potted plants a number of cuttings were also run to enable a comparison between cuttings and potted plants of the same species.

With the potted plants it is noteworthy that, with but a single exception, the period of maximum transpiration was reached at the time of maximum evaporating power of the air, a little before the middle of the afternoon. The graphs of evaporating power of the air and those of transpiration of potted plants are very similar. Per unit area, however, between three and five times as much

water is evaporated from a free water surface as from leaf surface on hot days.

With cuttings somewhat different results were obtained. With occasional exceptions, especially on less extreme days, the maximum daily transpiration was reached before noon, 2–4 hours before that

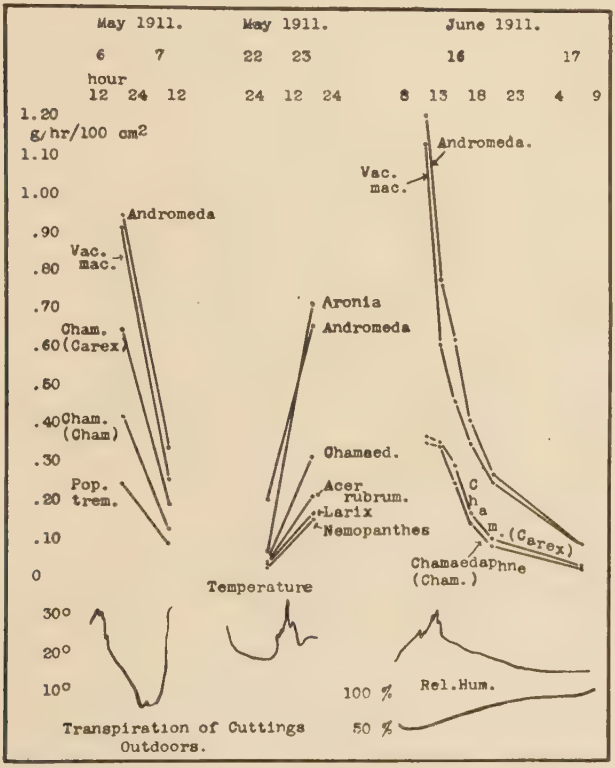

FIG. 7.—Transpiration of cuttings of *Acer rubrum*, *Andromeda glaucophylla*, *Aronia melanocarpa*, *Chamaedaphne calyculata* (from both the *Carex* and the *Chamaedaphne* associations), *Larix laricina*, *Nemopanthes mucronata*, *Populus tremuloides*, and *Vaccinium macrocarpon* outdoors.

of the maximum evaporating power of the air. Exceptions were more general in shrubs and especially in *Chamaedaphne*. In this species, whose rate of transpiration is low at all times, even in cuttings, the maximum transpiration accorded closely with the maximum evaporating power of the air.

A comparison of the results of potted plants and cuttings of the same species, although exhibiting some variation, shows that the rate of transpiration is greater in the potted plant. The difference is usually greatest at the time of maximum evaporating power of the air. Under less extreme conditions of evaporation, the

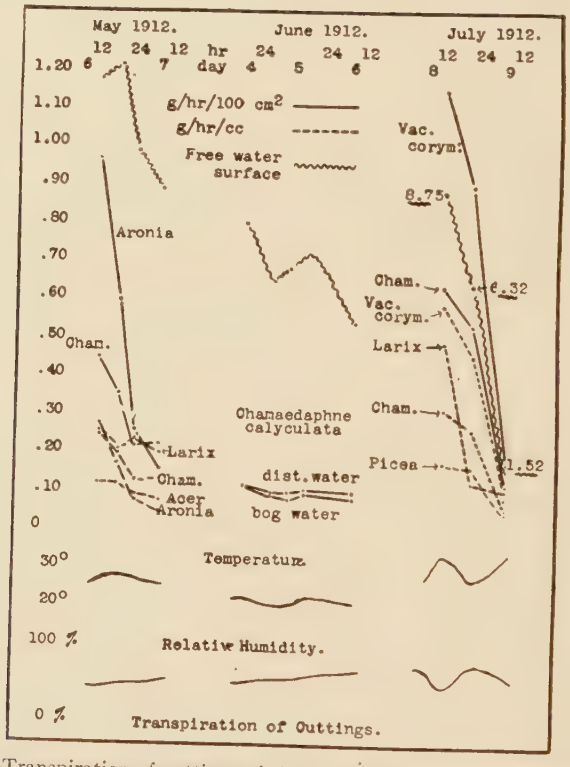

FIG. 8.—Transpiration of cuttings of *Acer rubrum*, *Aronia melanocarpa*, *Chamaedaphne calyculata*, *Larix laricina*, *Picea mariana*, and *Vaccinium corymbosum* outdoors, and of cuttings of *Chamaedaphne calyculata* from bog and distilled water in the laboratory.

graphs of transpiration of cuttings accord more closely with those of potted plants. From this it follows that one can obtain a knowledge of relative values under moderate conditions with cuttings, but experimentation under extreme conditions of evaporating power of the air with cuttings is unsatisfactory.

From an inspection of all of the summer data, it is seen that

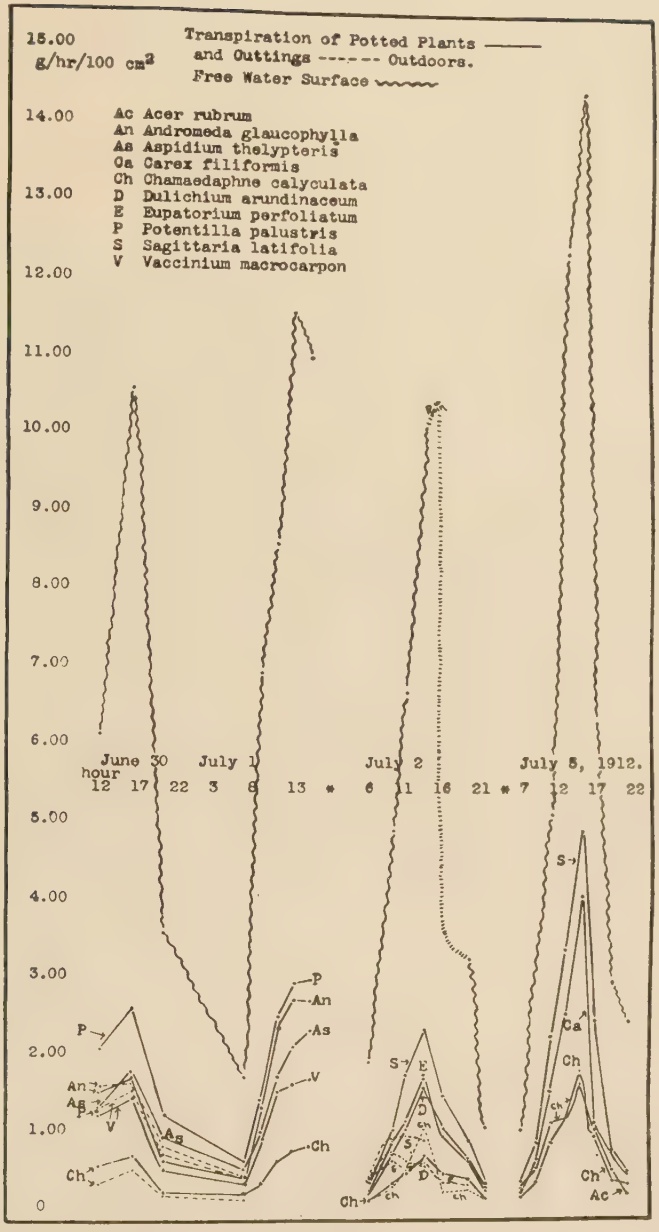

FIG. 9.—Transpiration of certain potted plants and cuttings during a severe hot wave.

among the shrubs, *Chamaedaphne* exhibits the lowest rate of transpiration. Herbaceous plants in general show a higher rate of transpiration than shrubs, while trees usually have a lower rate. Among plants that may be exposed to winter conditions, evergreen trees and shrubs transpire at a lower rate than deciduous trees and shrubs.

FIG. 10.—A view of potted plants and cuttings in the course of a transpiration experiment during a hot wave; July 2, 1912.

Rate of conduction

For use in these experiments cuttings were made in the evening after the stomates had closed, and kept under laboratory conditions over night, where the sun could strike them in the early morning, after which the experimentation was carried on as usual. Consequently, the results are not maximum rates of conduction, but relative rates of different species under similar conditions. In the summary of this work (table V), each set of

experiments is grouped together, and each figure represents at least two determinations.

TABLE V

SUMMARY OF SUMMER EXPERIMENTATION (1912) ON RATE OF CONDUCTION OF PEAT BOG PLANTS; RESULTS IN CENTIMETERS PER HOUR

	July 6	July 6	July 8	July 9
Temperature	31°	33°	25°	26°
Relative humidity	59 per cent	48 per cent	69 per cent	69 per cent
Chamaedaphne calyculata	12	20	13	22
Andromeda glaucophylla	21	.....	.....	.....
Vaccinium macrocarpon	23	.....	.....	.....
Vaccinium corymbosum	.....	.....	60	.....
Larix laricina	(31*)	.....	47	.....
Picea mariana	.....	.....	26	.....
Acer rubrum	.....	70	.....	.....
Cephalanthus occidentalis	(27*)	(140*)	.....	(170*)
Aronia melanocarpa	(51*)	.....	.....	108
Salix pedicellaris	(35*)	.....	.....	.....
Nemopanthes mucronata	(40*)	.....	.....	.....
Spiraea salicifolia	.....	48	.....	.....
Sambucus canadensis	.....	.....	.....	180
Aspidium thelypteris	(30*)	.....	.....	66
Asclepias incarnata	.....	.....	.....	210
Eupatorium perfoliatum (wilted)	.....	.....	.....	84
Sagittaria latifolia (wilted)	.....	.....	.....	49
Hypericum virginicum	.....	.....	.....	126
Potentilla palustris	.....	.....	.....	86
Typha latifolia	.....	.....	.....	114
Carex filiformis	.....	.....	.....	90
Sarracenia purpurea	.....	.....	.....	102

*Figures followed by an asterisk and inclosed in parentheses indicate that the lithium nitrate had reached the tip of the stem within the time of experimentation.

From an inspection of the data of table V it is readily seen that the evergreen ericads experimented with are all characterized by a low rate of conduction, decidedly low in comparison with that of both herbaceous plants and other shrubs. The rate of conduction was markedly lower in the evergreen bog trees than it was in the deciduous bog trees. Southern swamp shrubs showed a higher rate of conduction than northern bog ones.

Relation of summer to the xerophily of peat bog ericads

During the summer all the peat bog plants are actively carrying on the work of the growing season and have their greatest need of water. Especially at the beginning of the growing season the soil

water is cold, more so in the tree and shrub associations than in the herbaceous ones. This necessitates conservation of water and consequently xerophytic adaptation. Leaves that are produced in a time of drought (June 1912 at Mud Lake) are more xerophytic, in that they remain upright, than those produced under normal conditions (May 1912 at First Sister Lake, fig. 11). Neither observations in the extreme summer drought of 1911 in Cheboygan

FIG. 11.—*Chamaedaphne calyculata* in bloom at First Sister Lake; May 6, 1912

County, Michigan, nor experimentation under severer conditions than obtain in nature made it apparent that such a degree of xeromorphism as exhibited by *Chamaedaphne* was necessitated by the summer conditions alone.

ABSORPTION OF WATER VAPOR FROM A SATURATED ATMOSPHERE

From the increases in weight repeatedly obtained while experimenting with potted plants and cuttings of ericads during times of high relative humidity, it seemed necessary to assume the ability to absorb a measurable amount of water from the water vapor in the air, at a time when the evaporating power of the air was low. During June and July 1912, some measurements were made of the

changes in weight which took place when leafy twigs were subjected to dry air and moist air under bell jars. A twig of *Chamaedaphne* which lost water at the rate of 0.026 gm. per hour per 100 sq. cm. of leaf surface in dry air, while under a bell jar with a dish of water gained at the rate of 0.010 gm. Twigs of *Picea mariana* and *Larix laricina* gained in weight in moist air at the rate of 0.00027 and 0.000034; while those in dry air lost at the rate of 0.0061 and 0.0111 gm. per hour per cc. of volume, respectively.

These experiments demonstrate the ability of the living leaves of the three evergreen ericads and two conifers used to absorb water vapor in measurable quantities from saturated air. The amount so absorbed has increased the weight of a leafy twig by 6 per cent in 4.5 hours. When one considers the low position of bogs and the presence of heavy dew practically every night, no inconsiderable quantity of water may be accumulated in this way and furnish a part of the water for evaporation during the day and so lessen the demand upon the roots.

Dead leaves of *Chamaedaphne* absorb considerably more (3–6 times) than living ones. The scales which are present in abundance on the lower sides of the leaves no doubt take an active part in this absorption. Their structure is very similar to those of certain epiphytic orchids (*Vriesia*) which have been shown to be water-absorbing.

This function may serve to explain the excessive abundance of scales produced on the leaves developing in the excessively dry month of June 1912 at Mud Lake, in opposition to the smaller number on the leaves of the plants at First Sister Lake which developed in May before drought conditions set in.

The lessening of the drain upon the root system, when absorption is at best difficult, is no doubt greatly assisted by vapor absorption by the leaves. The prevalence of dew and frost in the bogs even when absent on the uplands indicates the greater humidity of the bog conditions. The actual presence of snow in contact with the leaves greatly aids in two ways: in checking water loss, and in constantly furnishing water vapor which may be absorbed.

The effect of absence of snow protection in time of cold, dry weather was admirably shown in the vicinity of Ann Arbor during

the winter of 1911–1912 (GATES 19). The bushes of *Chamaedaphne* were uniformly killed down to the snow level. This might have been due to the cold itself, but more likely was the result of excessive drying beyond the limits of the plants to recuperate. The difference in temperature at the snow level and 3 cm. below it was scarcely noticeable, upon the occasions when it was determined, during the moderately cold weather (−15 to 20°), yet above the snow line the plants died. At low temperatures the absolute amount of water vapor that can be in the air is very low, but below the line of snow the air is saturated. This argues for death by drying rather than by freezing, for the leaves below the snow line have more chance to keep within the drying limits of their protoplasm.

EXPERIMENTATION UPON THE CONDITION OF THE STOMATES

As has already been outlined, the data obtained upon this question are based upon the time it took a penetrating liquid (xylol) to render the leaf translucent. Different species varied in the readiness with which they became translucent, but a little experimentation soon sufficed to disclose a "normal" rate upon which to base deductions.

During the entire course of the experiments upon the several species of bog plants, the relative time of penetration indicated that the stomates were always open during the time that the full sun shone upon them. For many plants the diffuse light of early morning was sufficient to open the stomates partially, but it did not always appear that they were wide open until the full sun shone upon them. In other species, as *Nymphaea advena*, the stomates did not open until the direct sun reached the leaves. So far as was observed, clouds did not cause the closing of the stomates on hot, dry days, but on cloudy days the stomates closed earlier in the afternoon than on sunny days.

Just after the time of maximum transpiration and maximum evaporating power of the air, the stomates begin to close. The rate of transpiration drops very quickly, but stomates close slowly, and in most of the species are not completely closed until after dark. In a few species, as *Salix pedicellaris*, there was no evidence that the stomates ever closed.

Plants that were collected in the morning always had their stomates wide open at the time of collection. Before the laboratory was reached, however, the plants were frequently wilted, and investigation always showed the stomates closed. If not too severely wilted, the plants survived within an hour after cutting under water under laboratory conditions of diffuse light. When revived, the stomates opened partially in the diffuse light, but opened wide when exposed to sunlight.

Collections in the early afternoon of summer days were abandoned because of the difficulty of getting the material into the laboratory without extreme wilting. At this time of day the stomates were always wide open in the field, but closed upon wilting.

Collections made just before dark showed different results for different plants. The sun no longer shone upon the leaves, although it was by no means dark. Most of the leaves were very slowly penetrated by the xylol, which indicated that the stomates were but partially open. In some species (*Nymphaea*) the stomates were closed tight and no penetration would take place even in two minutes.

Some experimentation was performed on material kept in the laboratory with the following results. Wilted plants (*Aspidium thelypteris*, *Dulichium arundinaceum*, *Menyanthes trifoliata*, *Nymphaea advena*, *Potentilla palustris*, *Eupatorium perfoliatum*, *Acer rubrum*, *Spiraea salicifolia*, and *Vaccinium macrocarpon*) invariably had their stomates closed, as the length of time it took the xylol to penetrate the leaves testified. One single exception was found to be *Salix pedicellaris*, in which there was a scarcely perceptible increase in the time of penetration of wilted specimens as compared with plants in the field. If wilting was allowed to continue until the leaves became dry, the almost instantaneous penetration gave proof of the open condition of the stomates in the material used (*Spiraea salicifolia*, *Nemopanthes mucronata*, *Aronia melanocarpa*, *Salix pedicellaris*, *Chamaedaphne calyculata*, *Potentilla palustris*, *Ilex verticillata*, *Cephalanthus occidentalis*, *Menyanthes trifoliata*, *Carex filiformis*, and *Larix laricina*). Those of *Gaylussacia baccata* were only partially open.

Leaves of *Salix pedicellaris*, *Andromeda glaucophylla*, *Chamae-*

daphne calyculata, *Aronia melanocarpa*, *Potentilla palustris*, *Acer rubrum*, and *Cicuta maculata* were kept in the laboratory window submerged in water for a couple of days. Xylol determinations disclosed the fact that the stomates were open both day and night. Only in *Chamaedaphne* was there a perceptibly longer penetration time after dark than in the day.

This method of experimentation upon living plants in the field, which gives results so very quickly, leads to the view that stomatal movements and variations of the rate of transpiration are to a high degree independent of each other. Light is the fundamental cause for change in the first and the evaporating power of the air in the latter. The fact that the maximum evaporating power of the air occurs during the period of light does not necessarily mean that the stomates regulate transpiration. It has been shown that transpiration can change independently of stomatal movement (LLOYD 32). BROWN and ESCOMBE (53) have shown that the outward diffusion of water vapor observed is not as great as the capacity of the stomates will permit. The check in transpiration during the day comes with decline of the evaporating power of the air, and the stomates begin to close *soon after*, with the diminishing light intensity. There is no doubt that closed stomates retard water loss, and that stomatal movements and transpiration changes often occur in conjunction; but that is not proof that one is the cause and the other its effect.

Conclusions

Water loss was demonstrated in every plant experimented with during the winter as well as during the summer. During the low temperatures of winter this water loss was very low, although it continued to take place even when the water was frozen around the stem. Either this water loss was a permanent drain on the water content of the stem or, as the experiments on conduction showed, there was a certain amount of renewal from the external frozen solution. Whether a plant can obtain water directly from an ice surface is not known, but it has been shown by KOSAROFF (25) and others that plant roots can absorb water vapor when the temperature is below freezing. The amounts, though small, are

usually sufficient to satisfy the needs of the plants. In nature, the ground, although often frozen to a slight depth, is usually protected by a snow cover during the winter (fig. 12). The spaces between the snow particles are saturated with water vapor. This produces a blanket effect, greatly reducing the temperature changes beneath the snow level and tending to keep the temperature nearer the freezing point in times of cold. Evaporation from the snow also furnishes an available form of water in winter.

FIG. 12.—A view in the Mud Lake bog when *Chamaedaphne* was buried under 80 cm. of snow; March 26, 1912.

The evergreen ericads are distinctly grouped apart from the deciduous plants. The transpiration of the former in winter was 2–15 times as great as in the latter. The evergreen habit, even with a noteworthy accumulation of recognized xerophytic structures, was not as efficient a protection as the deciduous habit. This the universal killing of the plants of *Chamaedaphne* above the snow line in the extremely severe winter of 1911–1912 demonstrated, while other evergreen plants, not so intensely xeromorphic, but entirely covered with snow, were unharmed.

During the summer the water loss was much greater than in the

winter, especially, to be sure, in plants of the deciduous habit. Transpiration bore a rather definite relation to the evaporating power of the air. This relation varied both with species and with individuals. Its numerical value was from one-third to one-twelfth that of the air. It was obvious how efficient the xeromorphic structure of the evergreen trees and shrubs is in lowering the rate of transpiration during the summer. During the winter the absolute value of transpiration of *Chamaedaphne* varied up to 0.02 gm. per hour per 100 sq. cm. of leaf surface as a maximum under outdoor conditions, and 0.07 gm. under indoor conditions, and did not exceed 0.30 gm. under conditions above a hot radiator, which were severer than ever experienced in nature. Transpiration from distilled water was 1.09 times that from bog water. During the summer the normal rate at night is less than 0.10 gm., while in the daytime it approaches 0.80 gm. Only on extremely hot days with low relative humidity did the rate exceed 1.00 gm. The maximum recorded was 1.70 gm./hr./100 sq. cm. This means that the average summer rate of transpiration in *Chamaedaphne calyculata* is 25–30 times greater than the maximum winter rate, while the maximum summer rate was over 80 times that of the maximum winter rate. For deciduous plants the difference is very much greater.

The highest rates of water loss were in the more hydrophytic plants, *Nymphaea advena*, *Sagittaria latifolia*, and *Carex filiformis*, which agrees with the experimental data obtained by Otis (36) by a different method. In a potted plant of *Sagittaria* the maximum rate obtained during the investigation occurred on the afternoon of July 5, 1912 (4.82 gm./hr./100 sq. cm.).

As has been stated above and is here briefly repeated, during the winter the transpiration and rate of conduction of water are much higher in the evergreen plants (*Chamaedaphne calyculata*, *Andromeda glaucophylla*, *Vaccinium macrocarpon*, and *Picea mariana*) than in the deciduous ones. In the summer the rate of transpiration and conduction in the herbaceous plants (*Nymphaea advena*, *Sagittaria latifolia*, *Eupatorium perfoliatum*, *Asclepias incarnata*, *Dulichium arundinaceum*, *Aspidium thelypteris*, *Hypericum virginicum*, *Carex filiformis*, *Cicuta maculata*, and *Potentilla*

palustris) and in the deciduous woody plants (*Aronia melanocarpa*, *Nemopanthes mucronata*, *Salix pedicellaris*, *Cephalanthus occidentalis*, *Spiraea salicifolia*, *Gaylussacia baccata*, *Vaccinium corymbosum*, and *Larix laricina*) is much higher than in the evergreen shrubs and trees. The more xeromorphic the structure of the leaves the lower is the transpiration, and the more exposed to winter conditions the more xerophytic is the structure. This argues well for the winter conditions as being the fundamental causes necessitating xerophily in the evergreen ericads. The difficulty is in not being able to obtain water sufficiently fast or in sufficient quantities to supply the demands of transpiration. This is very much accentuated in the winter, mainly on account of low temperatures.

Although this xerophytic structure also reduces the water demands of these plants during the summer, there does not appear to be in summer any need of so thorough a xerophily, for neither the very extreme droughts and hot spells of the summers of 1911 and 1912, nor the extreme evaporating conditions of the laboratory appreciably injured the many plants of *Chamaedaphne* observed or experimented upon. On the other hand, the continued severe dry cold during the winter of 1911–1912 killed thousands of plants of *Chamaedaphne* down to the snow line, below which they were efficiently protected, whereas during the average winter of 1910–1911, with but very little snow on the ground during the coldest weather (barely below $-17°$ C.), all of the bushes of *Chamaedaphne* remained alive clear to the top.

As these ericads are of distinctly northern phytogeographic affinities (Harshberger **21, 22,** and Transeau **48**), and consequently are less subject to the extremes of summer conditions which obtain near Ann Arbor, almost at the southern limit of their range, and are more subject to severe winter conditions in nature farther north, and as the evergreen habit is a hereditary character, the xerophytism is real and has been brought about and is necessitated primarily by the winter conditions which these plants endure.

Summary

1. The determination of the rate of transpiration per unit area of leaf surface by weighing is a satisfactory approach to a knowledge

of the demands of plants for water, one of the most essential features of their environment. This unit was taken as grams per hour per 100 sq. cm. of leaf surface.

2. While the use of rooted plants is most desirable, the results obtained through measuring the transpiration of cuttings, the stomates of which are closed at the time of collecting and during the period of adjustment to the apparatus, approach closely those of potted plants, except under extreme conditions of evaporating power of the air. Experiments run in duplicate are a check upon the behavior of individual specimens.

3. Cuttings of hydrophytic plants wilt in a very short time in spite of every precaution, and experiments of any duration cannot be made upon them. Cuttings of other herbaceous plants, if properly cared for, may be used for at least 24 hours, and cuttings of shrubs and trees may be used for a still longer time.

4. From the data obtained in this investigation, transpiration varies with the evaporating power of the air, that is, increases directly with increase of temperature, decrease of relative humidity, increase of air movement, and, other factors being equal, is greater in daylight than in darkness. The last factor, however, is due to the tendency toward increased internal temperature with absorption of radiant energy.

5. The transpiration of all plants experimented with was very low in winter, yet was demonstrable during the daytime of clear days, even at the lowest temperatures ($-29°$). Very frequently no transpiration could be detected during the night. The decided gain in weight which frequently occurred is to be attributed to the power possessed by the leaves of these evergreen ericads of absorbing water from a humid atmosphere. A gain always occurred on frosty nights and at times of high relative humidity. Both fresh and dried twigs of the evergreen ericads and of the conifers exhibited an ability to absorb water vapor from humid air. Such absorption is much greater in quantity per unit volume of leafy twig in the evergreen conifer *Picea mariana* than in the deciduous conifer *Larix laricina*, and in the scale-covered *Chamaedaphne* than in the other evergreen ericads. As such absorption not infrequently is three or four times as great as the transpiration

during a very cold winter day, it is obvious how great is the advantage of this ability to lessen the demands upon the root and conducting systems at a time when the ground is frozen solid.

6. The transpiration per unit surface of the evergreen shrubs was very decidedly greater (4–10–30 and more times) than that of the deciduous shrubs during the winter under both outdoor conditions and indoor conditions which simulated warm spells in winter.

7. Among the evergreen ericads the relative rates of transpiration varied in the inverse order of their exposure and of their xerophytic structure. *Chamaedaphne*, which is the most exposed and the most xerophytic, has the lowest rates of transpiration and conduction.

8. During an average southern Michigan winter, protection by snow is not essential to the preservation of *Chamaedaphne*. In an extremely severe winter (1911–1912) absence of snow protection results in the killing of parts not so protected.

9. During the coldest weather (−29°) it did not appear that twigs or leaves of *Chamaedaphne* were frozen, as they were either perfectly pliable to handling or cracked as dry leaves.

10. Experimentation upon the rate of conduction by the lithium nitrate method showed a relatively higher rate at first, following the shock of cutting. Variations in external factors could not be arranged for a given plant because the shortness of the stem necessitated a short time of experimentation, and in order to obtain the data the stem had to be destroyed.

11. The rate of conduction was faster from warmer solutions, but was never zero when the solution was frozen. As the transpiration varied similarly, it seems obvious that the transpiration exercises a general regulatory function on the rate of conduction, similar to that which it exercises upon water absorption. The regulation is not exact, for in incipiently dry plants the rate of absorption and conduction is relatively greater than the rate of transpiration, while in turgid plants transpiration may be greater than absorption or conduction.

12. While the rate of conduction was relatively higher in the evergreen ericads than in other shrubs during the winter, leafless

twigs of *Larix* exhibited virtually as high a rate of conduction, especially from colder solutions.

13. From the experimentation it appears that the rate of conduction is ample to the needs of these plants for temperatures above $-15°$ (and probably above $-20°$).

14. The transpiration of all plants experimented with in summer was very decidedly greater than in winter. This was most marked in deciduous species and least so in evergreen species.

15. Under summer conditions, hydrophytes exhibited the highest transpiration per unit area of leaf surface. In general, herbaceous plants transpired at a higher rate than shrubs. The more hydrophytic swamp shrubs transpired at a higher rate than the typical bog shrubs. The evergreen shrubs transpired at a very distinctly lower rate than the deciduous ones. Among the bog trees the lowest rates occurred in the evergreen species. The rate of the deciduous conifer *Larix laricina* was noticeably higher than that of the deciduous broad leaf tree *Acer rubrum*, and was decidedly higher than that of the evergreen conifer *Picea mariana*.

16. The rate of conduction under summer conditions was very high in comparison to that under winter conditions. This was less noticeable in the evergreen ericads than in other plants. The summer rate in *Chamaedaphne* was but 10–20 times that of the winter rate. The maximum rate obtained under conditions of experimentation which were not extreme was 23 cm. per hour in an evergreen ericad, while rates above 100 cm. per hour were frequently found in other shrubs and in herbaceous plants. An evergreen bog tree, *Picea mariana*, exhibited a distinctly lower rate of conduction than deciduous trees whether conifer or hardwood.

17. In the case of peat bog plants in nature, light (particularly sunlight) seems to be the effective factor in causing stomatal movements. Stomatal movements, while effective regulators of transpiration when they occur, do not appear so closely to regulate transpiration of peat bog plants as the evaporating power of the air.

18. In view of the fact that exposure to the very extreme summer conditions in 1911 and 1912 did not affect the vitality of the evergreen ericads, that neither did the average winter of 1910–1911, with its scanty snow covering during the coldest weather,

while the extreme winter of 1911–1912 killed the parts of the evergreen ericads which projected above the snow; and in view of the fact that the evergreen habit is hereditary, that the position of the leaves in winter is different from that in summer, and that the transpiration is decidedly less than that of deciduous shrubs and of herbaceous plants in summer but greater in winter, the xeromorphy of these plants is real xerophyty, occasioned fundamentally by the necessity of protection when exposed to winter conditions and used advantageously by these plants during the summer.

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